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When worlds collide: Invader-driven benthic habitat complexity alters predatory impacts of invasive and native predatory fishes

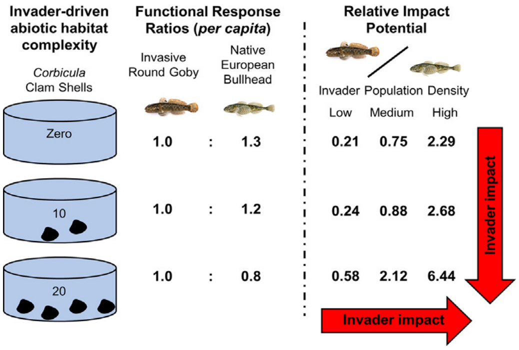
Neil E. Coughlan [a,b,*], James W.E. Dickey [b,c,d,e], Jaimie T.A. Dick [b], Vincent Médoc [f], Monica McCard [b], Gérard Lacroix [g,h], Sarah Fiorini [h], Alexis Millot [h], Ross N. Cuthbert [b]

[a] School of Biological, Earth & Environmental Sciences, University College Cork, Distillery Fields, North Mall, Cork, Ireland
[b] Institute for Global Food Security, School of Biological Sciences, Queen's University Belfast, 19 Chlorine Gardens, Belfast, Northern Ireland BT9 5DL, UK
[c] Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB), 12587 Berlin, Germany
[d] Freie Universität Berlin, Institute of Biology, Königin-Luise-Str. 1-3, 14195 Berlin, Germany
[e] GEOMAR Helmholtz-Zentrum für Ozeanforschung Kiel, 24105 Kiel, Germany
[f] Equipe Neuro Ethologie Sensorielle, ENES/Neuro-PSI CNRS UMR 9197, Université de Lyon/Saint-Etienne, Saint-Etienne, France
[g] iEES-Paris, Institut d'Ecologie et des Sciences de l'Environnement de Paris, UMR 7618 (CNRS, INRAE, IRD, Sorbonne Université, UPEC, Université de Paris), CC237 Paris, France
[h] Ecole Normale Supérieure, PSL Research University, CNRS, Centre de Recherche en Écologie Expérimentale et Prédictive (CEREEP-Ecotron Ile-De-France), UAR 3194 Saint-Pierre-lès-Nemours, France

HIGHLIGHTS

- Invasive Corbicula clam shells significantly influenced predation by fish.
- Invader-driven benthic habitat complexity can stabilise fish feeding rates.
- Invasive goby, *N. melanostomus*, better tolerated shell-driven habitat complexity.
- Higher shell densities exacerbated the invader impact relative to native *C. gobio*.
- Invader-driven abiotic factors can underpin facilitative interactions.

GRAPHICAL ABSTRACT



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ABSTRACT

Interactions between multiple invasive alien species (IAS) might increase their ecological impacts, yet relatively few studies have attempted to quantify the effects of facilitative interactions on the success and impact of aquatic IAS. Further, the effect of abiotic factors, such as habitat structure, have lacked consideration in ecological impact prediction for many high-profile IAS, with most data acquired through simplified assessments that do not account for real environmental complexities. In the present study, we assessed a potential facilitative interaction between a predatory invasive fish, the Ponto-Caspian round goby (*Neogobius melanostomus*), and an invasive bivalve, the Asian clam (*Corbicula fluminea*). We compared *N. melanostomus* functional responses (feeding-rates under different prey densities) to a co-occurring endangered European native analogue fish, the bullhead (*Cottus gobio*), in the presence of increased levels of habitat complexity driven by the accumulation of dead *C. fluminea* biomass that persists within the environment (i.e. 0, 10, 20 empty bivalve shells). Habitat complexity significantly influenced predation, with consumption in the absence of shells being greater than where 10 or 20 shells were present. However, at the highest shell density, invasive *N. melanostomus* maximum feeding-rates and functional response ratios were substantially higher than those of native *C. gobio*. Further, the Relative Impact Potential metric, by combining per capita effects and population abundances, indicated that higher shell densities exacerbate the relative impact of the invader. It therefore appears that *N. melanostomus* can better tolerate higher IAS shell

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[*] Corresponding author at: School of Biological, Earth & Environmental Sciences, University College Cork, Distillery Fields, North Mall, Cork, Ireland.
E-mail address: neil.coughlan@ucc.ie (N.E. Coughlan).

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abundances when foraging at high prey densities, suggesting the occurrence of an important facilitative interaction. Our data are thus fully congruent with field data that link establishment success of *N. melanostomus* with the presence of *C. fluminea*. Overall, we show that invader-driven benthic habitat complexity can alter the feeding-rates and thus impacts of predatory fishes, and highlight the importance of inclusion of abiotic factors in impact prediction assessments for IAS.

1. Introduction

Invasive alien species (IAS) continue to spread and proliferate on a global scale, resulting in wide-ranging consequences that have detrimentally impacted biodiversity, ecosystem functioning, evolutionary dynamics, economies and food security (Ceballos et al., 2015; Turvey and Crees, 2019; Cuthbert et al., 2021). With the number of established IAS per continent predicted to increase substantially by 2050 (Seebens et al., 2021), understanding which species are likely to establish, spread, proliferate and exert ecological impact is vital (Dick et al., 2017b), especially in the context of environmental change (Zeng and Yeo, 2018; Dickey et al., 2021). Nevertheless, it remains difficult to ascertain the effects of emerging and existing IAS due to the highly context-dependent nature of invasions and their impacts (Dick et al., 2017a). In particular, further consideration of the role of biotic interactions, such as mutualisms and facilitation, in the success and impact of multiple IAS is urgently required (Crane et al., 2020), while the influence of abiotic factors, such as habitat structure, has rarely been considered in ecological impact prediction (but see Cuthbert et al., 2019a, 2019b; Gebauer et al., 2019; South et al., 2019). Facilitative interactions among invasive species are especially concerning as these species may promote their mutual establishment, persistence, as well as intensify impact on recipient ecosystems (i.e. invasional meltdown: Simberloff and Von Holle, 1999; Ricciardi, 2001; Crane et al., 2020).

Given their exposure to multiple transport pathways and the lack of effective biosecurity protocols, aquatic ecosystems are considered especially vulnerable to biological invasions (Piria et al., 2017; Coughlan et al., 2020b). Unlike terrestrial habitats, submerged aquatic environments are particularly difficult to monitor and, as a result, invasions are often well advanced before they become apparent (Beric and MacIsaac, 2015; Caffrey et al., 2016). Crucially, empirical evidence has begun to indicate that taxa from certain regions are predisposed to invasion success and impact in the aquatic realm (Cuthbert et al., 2020; Paiva et al., 2018; Dickey et al., 2021), with Ponto-Caspian taxa especially showing a considerable tendency to readily adapt to new environments (Ketelaars, 2004; Gallardo and Aldridge, 2015; Sturtevant et al., 2019). Further, facilitative interactions among Ponto-Caspian taxa have previously been observed, whereby the anti-predator protection provided by invasive zebra mussel (*Dreissena polymorpha*) shells was more effectively used by the invasive amphipod *Dikerogammarus villosus* than native gammarid species (Kobak et al., 2014). Equally, Ponto-Caspian *D. polymorpha* can alleviate competitive interactions between invasive macrophytes, facilitating shifts in dominance among closely related invaders (Crane et al., 2020).

The invasive Asian clam (*Corbicula fluminea*) is considered a high impact freshwater invader that can dominate macroinvertebrate communities, physically alter benthic habitats, and modify community and ecosystem dynamics through the formation of dense and expansive populations (Sousa et al., 2014). Now thought to be present across many of the major river basins in Europe and the Americas (Gama et al., 2017), predicted rates of climatic change will likely increase the availability of suitable habitat for *C. fluminea* within invaded and new river basins, especially at higher latitudes (Gama et al., 2017). Although extensive control and eradication experiments have been conducted on *C. fluminea*, none have successfully eliminated their populations (Caffrey et al., 2016; Coughlan et al., 2020a).

While the ecological impact of living invasive bivalves has received considerable scientific attention, relatively little is known about the impact of non-living biomass (McDowell and Sousa, 2019). This is despite the repeated mass mortality events that have been described for many invasive freshwater bivalves, including *C. fluminea* (Bódis et al., 2014; McDowell et al., 2017) and *D. polymorpha* (Churchill et al., 2017). A substantial quantity of empty shell biomass can also accumulate and persist over time within large healthy populations of invasive bivalves. In essence, the long-term accumulation of shells further promotes the role of invasive freshwater bivalves as ecosystem engineers through habitat creation and alteration (Sousa et al., 2009). Nevertheless, the impact of shell biomass on the trophic interactions of other organisms, such as predatory benthic fish, remains largely unknown. In particular, the extent to which the presence of augmented habitat structure via invasive bivalve shells could influence differences in ecological impacts between invasive and native predators requires study.

Originating from the Ponto-Caspian region, the round goby (*Neogobius melanostomus*) has become a widespread invader across Europe and the Great Lakes of North America, having shown considerable tolerance to a variety of abiotic stressors, such as temperature (Christensen et al., 2021), salinity (Behrens et al., 2017) and reduced dissolved oxygen (Arend et al., 2011; Dickey et al., 2021). Previous studies have, however, found substrate to alter feeding rates of *N. melanostomus*, whereby functional responses are dampened by sandy compared to gravel substrates (Gebauer et al., 2019). Impacts of *N. melanostomus* invasions include the exclusion of native species (Hempel et al., 2016) and trophic cascades ensuing from predation on invertebrates (Kipp and Ricciardi, 2012), with frequent reductions of native fish populations and the occurrence of total community replacements in European and North American waters (Van Kessel et al., 2016). The competitive superiority of *N. melanostomus* is considered a result of its aggressive behaviour, broad diet, greater adult size relative to many trophically-analogous native species and numerous spawning events, as well as parental care by males (Dubs and Corkum, 1996; Corkum et al., 2004; Bergstrom and Mensinger, 2009). In particular, the spread of *N. melanostomus* has been shown to be a substantial threat to smaller-bodied, trophically-analogous benthic freshwater fishes, such as *Cottus* species (Janssen and Jude, 2001; Van Kessel et al., 2016). For example, laboratory studies indicate that *N. melanostomus* tends to be a more efficient predator than the endangered European bullhead (*Cottus gobio*) at low dissolved oxygen levels (Dickey et al., 2021). Although *C. gobio* has been threatened by a number of anthropogenic factors, including pollution and purposefully stocked invasive fish (Utzinger et al., 2008; Lorenzoni et al., 2018), long-term monitoring suggests that *N. melanostomus* populations have little effect on the abundance of *C. gobio* (Janáč et al., 2018). However, it has been suggested that regional effects, possibly linked to physical habitat structure, may modulate this relationship (Janáč et al., 2018).

In the present study, we assessed the potential ecological impact of *N. melanostomus* relative to *C. gobio* under three habitat complexity treatments that consisted of either 0, 10 or 20 shells of dead *C. fluminea*. Shell biomass was included to aid understanding of how the feeding efficiency of both species might vary in the presence of habitat complexity from another invasive trophic group. Further, as the potential effects of empty *C. fluminea* shells on predator-prey interactions are unknown, we sought to determine the existence of any emergent effects of their shell biomass within aquatic systems, including facilitative interactions that potentially worsen invader impacts relative to natives. To achieve this, we used the comparative functional response approach (CFR: Dick et al., 2014, 2017a), which employs the classic metric of the functional response (FR: Solomon, 1949; Holling, 1959) to quantify how prey density influences predator consumption rates. The CFR method has been successfully used to quantify ecological impact, predict population stability implications, and has consistently explained how damaging invaders have greater impacts than native trophic analogues often across a myriad of biotic and abiotic context-dependencies, including oxygen depletion (e.g. Dickey et al., 2021; Cunningham et al., 2021). Moreover, we then combine functional response maximum feeding rates (i.e. per capita feeding) with estimated predator field abundances (a proxy for the numerical response) to quantify the "Relative Impact Potential" between these fishes under different fish and shell density scenarios (Dick et al., 2017b). Overall, we hypothesise that the Ponto-Caspian invader will have a higher impact than the native species with respect to habitat complexities. Nevertheless, we expected that increased numbers of shells will reduce interaction strengths and stabilise FR form, as greater levels of habitat complexity will likely decrease the predator attack rates and increase their prey handling time.

2. Methods

2.1. Animal collection and maintenance

The invasive round goby, *Neogobius melanostomus,* was collected on the 6th of October 2018 from the Moselle River at Koenigsmacker, Moselle, France (49°24′14.6″N 6°15′24.3″E), while the native bullhead, *Cottus gobio*, was collected on the 4th of October 2018 from the Ru du Dragon, Longueville, France (48°31′20.4″N 3°14′22.3″E). Both species were sampled via electrofishing (n = 40 ind. species^{-1}). It was not possible to obtain both fish species in adequate abundances from the same site. Fishes were transported in continuously aerated source water and housed separately in a laboratory at CEREEP Ecotron Île-De-France (Saint-Pierre-lès-Nemours, France) in opaque 250-L drums containing continuously aerated, 50-μm-filtered lake water acquired on site (280 μS; 8.5 pH). A full water change was performed every second day within each drum. Fish selected for the experiment were matched as closely as possible with respect to total length (TL mean ± SD: goby = 83.0 ± 5.45 mm; bullhead = 80.4 ± 3.41 mm) and mouth gape height (GH mean ± SD: goby = 7.12 ± 0.97 mm; bullhead = 8.3 ± 0.62 mm) to, as far as possible, quantify species-specific differences unrelated to fish size and mouth gape. A standard diet of commercially-purchased frozen chironomid larvae was provided ad libitum. Fish were reused systematically in experiments following a designated recovery time (≥48 h) under standard diet and housing conditions (as per Alexander et al., 2015), whereby each individual was used a maximum of two times and only once within each prey density in each habitat complexity as detailed below. Reuse helped minimise the number of individuals required, especially of the endangered native bullhead (see also Ethics statement).

The experimental prey, the amphipod *Echinogammarus berilloni* (TL: 5–8 mm), known to be consumed by both species in the field and in the lab (Laverty et al., 2017), and representative of the diet of both fish species, were collected from Le Lunain River, Nonville, France (48°17′24.0″N 2°47′20.6″E), via kick sampling and transported in source water to a laboratory at CEREEP Ecotron Île-De-France (19 ± 2 °C). These prey were maintained on a diet of source stream flora and fauna ad libitum in 7-L containers containing continuously aerated, filtered lake water. Empty *C. fluminea*, shells were collected by hand from the Seine River, Moret-Loing-et-Orvanne, France (48°23′14.9″N 2°47′30.6″E), and transported to a laboratory at CEREEP Ecotron Île-De-France. Only undamaged shells were selected for inclusion within the experiment (shell height: 19.88 ± 2.73 mm, 14–28.7 mm; mean ± SD, min.–max.).

2.2. Functional responses (FRs)

The FRs of both fish species were quantified at three habitat complexity regimes over six prey densities. Habitat regimes consisted of a 1 cm deep flat layer of commercially purchased sand (Fontainebleau-ultrapure siliceous sand (97–99 % of silica), grain size <350 μm), with either 0, 10 or 20 single valve *C. fluminea* shells. Sand was provided for basic habitat simulation, and previous studies have shown gobies to feed readily under these conditions (Gebauer et al., 2019). Single shell valves were used, as shells of dead *C. fluminea* residing on the benthic surface are generally found in an open position once the soft tissue of the bivalve has decomposed, often with the valves detaching from one another, i.e. the two valves that form the shell in its entirety eventually tend to break apart from their hinge point. Single shell valves were gently placed in the sand substrate, with half facing upwards, i.e. external surface on the sand, and half facing downwards, i.e. with their internal surface facing the sand. Shells with their inner surface facing sand were gently pushed downwards to eliminate gaps between the shell edge and substrate. Treatments were fully randomised spatially and temporally to eliminate block effects.

Prior to FR experiments, fish were starved separately for 24 h in the laboratory (19 ± 2 °C; 12:12 light regime) to standardise hunger levels. Following starvation, fish were introduced individually to 7-L opaque polypropylene arenas (33.5 × 24.5 cm) containing the constructed habitat regimes and filtered lake water, and were allowed to acclimatise for 2.5 h. *Echinogammarus berilloni* prey were added to 2-L arenas with filtered lake water at each of six densities (2, 4, 8, 16, 32 and 64). The experiment was run at 19 °C under the three levels of habitat complexity above, i.e. 0, 10 and 20*C. fluminea* shells. Each combination of prey density and habitat complexity was replicated three times (i.e., $n = 3$ per treatment group). Trials were initiated following the addition of designated prey densities to each experimental unit, with fish allowed to feed subsequently for 1 h. Controls consisted of a replicate under each level of 'habitat regime' and 'prey density' to account for any potential background prey mortality. Following the feeding period, fishes were removed and remaining live prey counted to derive prey numbers consumed. No partial prey consumption was observed.

2.3. Statistical methods

Statistical analyses were undertaken in R v4.0.2 (R Core Team, 2020). Functional response analyses were undertaken with the 'frair' package in R (Pritchard et al., 2017), which allows selection, fitting and comparisons among common functional response models and constituent parameters based on the prey density and associated consumption values derived from our comparative functional response experiments. Generalised linear models assuming a binomial error distribution were used to infer FR types, with proportional prey consumption modelled as a function of initial prey density, separately for each of the six predator and habitat combinations. Here, a significantly negative linear coefficient is indicative of a Type II FR (Juliano, 2001) and significant positive and negative linear and quadratic coefficients, respectively, indicate Type III FR. To account for non-replacement of prey during the experiment, we used Rogers' random predator equation for prey depletion to model FRs (Rogers, 1972):

$$N_e = N_0(1 - \exp(a(N_e h - T))) \tag{1}$$

where N_e is the number of prey eaten, N_0 is the initial density of prey, a is the attack rate, h is the handling time and T is the total experimental period. Maximum feeding rates ($1/h$) were also calculated. The Lambert W function was implemented to make Eq. (1) solvable (Bolker, 2008). For each predator species, we subsequently employed the difference method to compare attack rate and handling time parameters pairwise according to habitat treatments (Juliano, 2001). Further, we calculated functional response ratios (FRR) by dividing the attack rate by the handling time within each treatment group to synthesise these parameters (Cuthbert et al., 2019c). Further, the Relative Impact Potential (RIP) metric was calculated to facilitate increased predictive power of ecological impact. The RIP metric combines the FR parameters (e.g. maximum feeding rate) with a proxy for the Numerical Response (NR: e.g. consumer abundance or density): RIP = ((FRinvader / FRnative) × (NRproxy of invader) / (NRproxy of native)) (see Dick et al., 2017b; Dickey et al., 2020). Densities of *N. melanostomus* across multiple invasion stages in the Moselle River were extracted from the literature (invasion front [low density] = 2.70 ind. m^{-2}; short-term invaded zone [moderate density] = 9.80 ind. m^{-2}; long-term invaded area [high-density] = 29.80 ind. m^{-2}: Masson et al., 2018). *Cottus gobio* density in the Ru du Dragon was 6.21 ind. m^{-2} (*Fédération de Seine-Et-Marne Pour La Pêche et la Protection du Milieu Aquatique*).

3. Results

Over 99.5 % of control prey survived, and thus gammarid prey deaths were attributed to predation by fish. All fish exhibited Type II FRs towards gammarid prey, irrespective of the presence of shells (Table 1; Fig. 1). For *N. melanostomus*, attack rates were higher in the absence of shells, with handling times tending to be shortest where shells were present in the highest abundance (Table 1). Where shells were absent, attack rates were significantly higher than in the presence of either 10 shells ($z = 2.66, p = 0.01$) or 20 shells ($z = 3.88, p < 0.001$), while there were no significant differences between 10 and 20 shell habitat treatments ($z = 1.12, p = 0.26$). On the other hand, handling times did not differ significantly for gobies across any habitat complexity levels (0–10: $z = 0.27, p = 0.79$; 0–20: $z = 1.28, p = 0.19$; 10–20: $z = 1.15, p = 0.25$).

For *C. gobio*, attack rates again were higher in the absence of shells, with handling times tending to be shorter at zero and low shell numbers (Table 1). Attack rates in the absence of shells were significantly higher than where 10 shells were present ($z = 2.66, p = 0.01$) as well as 20 shells ($z = 2.27, p = 0.02$), while there were no significant differences in attack rates between the presence of 10 and 20 shells ($z = 0.42, p = 0.67$). *Cottus gobio* handling times did not differ significantly according to habitat treatment between any shell levels (0–10: $z = 0.45, p = 0.65$; 0–20: $z = 1.36, p = 0.18$; 10–20: $z = 0.69, p = 0.49$).

Where shells were present in batches of 20, maximum feeding rates were substantially higher by *N. melanostomus* as compared to *C. gobio*. However, maximum feeding rates tended to be highest by *C. gobio* where shells were absent, or present in batches of 10 (Table 1; Fig. 1). A similar pattern was observed considering FRR between the species across the habitat treatments, indicating greater impact by the invader under high shell densities.

3.1. Relative impact potential

For all habitat complexity treatments, the highest population density of *N. melanostomus* exhibited an RIP > 1 (Table 2, Fig. 2). RIP values of 2.29, 2.68 and 6.44 were detected for habitat complexities of 0, 10 and 20*C. fluminea* shells, respectively. While a moderate density of *N. melanostomus* displayed an RIP > 1 for a habitat complexity of 20 *C. fluminea* shells (2.12: Table 2, Fig. 2), an RIP < 1 was calculated for moderate density of *N. melanostomus* under 0 and 10 *C. fluminea* shells (0.75 and 0.88, respectively). Similarly, a low density of *N. melanostomus* displayed an RIP < 1 across all habitat complexity treatments (0.21, 0.24, 0.58: Table 2, Fig. 2). The combination of high population density and high maximum feeding rate where shells were abundant indicate that *N. melanostomus* is predicted to have highest ecological impact when facilitated by *C. fluminea* (c.f. Fig. 2a–c).

4. Discussion

In the present study, we quantified the effect of invader-driven benthic habitat complexity on the feeding rates and predicted ecological impacts of invasive and native predatory fishes using the CFR and RIP methods. The Ponto-Caspian invader, *N. melanostomus* exhibited highest consumption rates at the highest invasive bivalve shell abundance, indicating a potential synergism that intensifies ecological impact compared to native species. This might reflect the co-evolutionary relationship between *N. melanostomus* and dense beds of functionally-similar *Dreissena* mussels (Kobak et al., 2016). *Cottus gobio* was observed to have higher maximum feeding rates and FRR values than *N. melanostomus* in the absence of shells, as well as at the lower shell abundance. Yet the inverse, whereby *N. melanostomus* had higher maximum feeding rates and FRR value, was recorded at the highest shell abundance. Although the higher feeding rates detected for *C. gobio* relative to *N. melanostomus* contradict previous studies, which consistently documented lower maximum feeding rates and FRR values for the native relative to the invader (e.g. Laverty et al., 2017; Dickey et al., 2021), these studies lacked basic habitat simulations and were devoid of differences in habitat structure. In the present study, even in the absence of shells, experimental aquaria had sandy substrates which have been shown to dampen feeding rates of *N. melanostomus* (Gebauer et al., 2019). Indeed, the feeding rate recorded for *C. gobio* in the absence of *C. fluminea* shells correspond to feeding rates determined for *C. gobio* under similar experimental conditions (e.g. Laverty et al., 2017; Dickey et al., 2021). In the presence of sand only, the feeding rate of *N. melanostomus* was contrastingly less than prey consumption rates previously recorded by comparable studies (Laverty et al., 2017; Dickey et al., 2021). Considering these results across studies, native *C. gobio* may thus be more robust to sandy substrates in the absence of other physical structures when predating.

Sand substrate was added to the base of all experimental arenas to provide a semblance of a basic habitat, whereas previous studies have tended to use bare plastic or glass arenas without additional enrichment. Although *C. gobio* tend to prefer coarse and stony substrate as opposed to fine sand (Prenda et al., 1997; Kakareko et al., 2016), the presence of sand and/or shells may have elicited sustained rather than reduced levels of foraging by *C. gobio* due to its preference for increased habitat complexity and tendency to seek shelter (Prenda et al., 1997; Kakareko et al., 2016). Nevertheless, as anticipated, increased numbers of *C. fluminea* shells did reduce prey consumption by both fishes, although reductions in fish attack rates were most pervasive, with alterations via increased handling times not being statistically clear. As such, the dampening effects of habitat structure were largely constrained to lower prey densities within fish species, corresponding a lessening of the initial slope of the FR curve, whereas feeding rates were relatively robust where prey were available at high densities for each predator given similarities in maximum feeding rates. Indeed, studies spanning a range of aquatic trophic groups have found habitat structure to consistently mediate trophic interaction strengths, promoting prey population stability and flattening the unimodal scaling between attack rates and predator-prey body mass ratios in benthic habitats, which is likely the result of reduced predator mobility or foraging efficacy (Barrios-O'Neill et al., 2016; Dunn and Hovel, 2020). Nevertheless, reductions in interaction strength at low prey densities with habitat complexity did not cause a categorical shift from a Type II to Type III FR here, as shown in other systems (e.g. Barrios-O'Neill et al., 2015). This thereby indicates relatively high rates of consumption at low prey densities under the habitat levels supplied for both fish species.

The Relative Impact Potential (RIP) metric reveals greater ecological impact by a high density of invasive *N. melanostomus* typical of long-term invaded sites, in combination with increased habitat complexity, i.e. facilitation among invaders. In effect, at a typical density ratio of 4.80 invaders to one native, *N. melanostomus* exhibits an ecological impact that ranged from 2.29 to 6.44 times greater than that of *C. gobio* across the assessed bivalve-driven habitat complexities (0–20 *C. fluminea* shells). While a

Table 1

Functional response linear coefficients and parameter estimates for the invasive round goby (*Neogobius melanostomus*) and native bullhead (*Cottus gobio*) feeding on gammarid prey in the presence of different habitat treatments, as well as functional response ratios (FRR; attack rate divided by handling time).

Predator	Habitat (shells)	Linear coefficient, p	Attack rate, p	Handling time, p	Maximum feeding rate	FRR
N. melanostomus	0	−0.041, <0.001	2.14, <0.001	0.038, <0.001	26.48	56.52
N. melanostomus	10	−0.015, 0.003	0.97, <0.001	0.041, <0.001	24.38	23.76
N. melanostomus	20	−0.011, 0.02	0.66, <0.001	0.024, 0.01	41.49	27.34
C. gobio	0	−0.016, <0.001	1.32, <0.001	0.018, <0.001	55.42	73.33
C. gobio	10	−0.010, 0.03	0.64, <0.001	0.023, 0.02	43.60	28.08
C. gobio	20	−0.016, 0.001	0.73, <0.001	0.032, 0.01	30.92	22.44

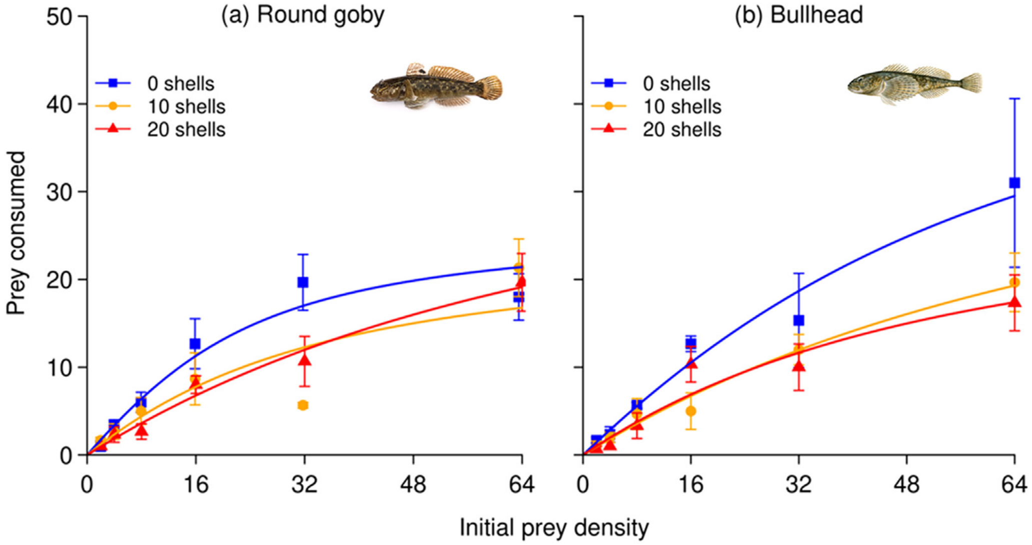

Fig. 1. Functional responses of (a) the invasive round goby (*Neogobius melanostomus*) and (b) the native bullhead (*Cottus gobio*) towards gammarid prey in the presence of different shell densities of dead *Corbicula fluminea* ($n = 3$ per treatment group). Means are ±SE.

moderate invader density (1.58:1.00, invader:native) showed more similar impact levels of 0.75 and 0.88 to that of the native at the lower habitat complexities, with an impact of 2.12 under the highest habitat complexity. The lowest invader density (0.44:1.00) displayed a comparatively reduced ecological impact across the assessed bivalve-driven habitat complexities (i.e. RIP of 0.21–0.58). This would suggest that the ecological impact of invasive *N. melanostomus* only becomes problematic at higher invader densities, with facilitation by bivalve shells when they are present in high numbers. Thus, the present study indicates that an increasing complexity of habitat structure, especially bivalve-driven habitat complexity, can exacerbate the population level effects of a predatory invasive fish. While this study demonstrates differences in top-down forces between these predatory fishes under different bivalve-driven habitat complexities, the wider impact of *C. fluminea* invasions on trophic interactions should also be considered. Particularly as the presence of invasive bivalves can alter trophic interactions through bottom-up forces (i.e. nutrient limitation), whereby the rate of primary production is reduced (Pagnucco et al., 2016), as well as facilitative interactions resulting in shifts in dominance among different species (Crane et al., 2020). Future studies should also consider multiple predator effects alongside habitat complexity treatments, such as potential intraspecific competitive interactions (Groen et al., 2012). In particular, intraspecific agonistic behaviours by *N. melanostomus* at higher densities might alleviate ecological impact.

Although the behavioural responses of the fishes in relation to habitat complexity need to be explored in greater detail, including through the more systematic alteration of predator-free space (Barrios-O'Neill et al., 2015), it appears that *C. gobio* may have a foraging advantage compared to *N. melanostomus* at low abundance of *C. fluminea* shells. Yet, this advantage seems to shift in favour of *N. melanostomus* at a higher abundance of *C. fluminea* shells. Given that *C. fluminea* form extensive and dense clam beds that can harbour a substantial amount of empty shells (Caffrey et al., 2016), *N. melanostomus* will likely derive a greater facilitative interaction with mature *C. fluminea* beds than *C. gobio*. Indeed, a variety of studies have tentatively linked the successful establishment of *N. melanostomus* with parallel invasions of various Mollusca, including *C. fluminea* (Dashinov and Uzunova, 2020). Primarily, as large adult *N. melanostomus* can consume molluscs (Polačik et al., 2009; Coughlan et al., 2017; Dashinov and Uzunova, 2020), while juvenile *N. melanostomus* appear to benefit from *Dreissena*-driven benthification of their nursery environments (Olson and Janssen, 2017). Facilitative interactions among *N. melanostomus* and high densities of invasive bivalves may lead to a negative community level effect in terms of invasional meltdown. Furthermore, increased habitat complexity will likely modify predator feeding rates through the provision of refugia, while eliciting different behavioural responses from predators in relation to their habitat preferences (e.g. Beekey et al., 2004). Accordingly, future work should consider behavioural change

Table 2
The Impact Potential (IP) and Relative Impact Potential (RIP) of the invasive species *N. melanostomus* relative to the native *C. gobio*, at three estimated invader densities, across three levels of habitat complexity (i.e. *Corbicula fluminea* shells). Impact Potential is calculated as the product of MFR (functional response maximum feeding rate: $1/h$: see Table 1) and density, with the RIP of an invader calculated as the $\left(\frac{FRinvader}{FRnative}\right) \times \left(\frac{DENinvader}{DENnative}\right)$.

Species	Invader-driven habitat complexity	MFR ($1/h$)	Density (ind·m^{-2})	Impact potential	Relative impact potential of IAS
N. melanostomus (low)	0 shells (0 ind·m^{-2})	26.48	2.70	71.48	0.21
N. melanostomus (medium)		26.48	9.80	259.46	0.75
N. melanostomus (high)		26.48	29.80	788.98	2.29
C. gobio		55.42	6.21	344.13	N/A
N. melanostomus (low)	10 shells (121.8 ind·m^{-2})	24.38	2.70	65.83	0.24
N. melanostomus (medium)		24.38	9.80	238.93	0.88
N. melanostomus (high)		24.38	29.80	726.55	2.68
C. gobio		43.60	6.21	270.74	N/A
N. melanostomus (low)	20 shells (243.7 ind·m^{-2})	41.49	2.70	112.02	0.58
N. melanostomus (medium)		41.49	9.80	406.57	2.12
N. melanostomus (high)		41.49	29.80	1236.31	6.44
C. gobio		30.92	6.21	191.99	N/A

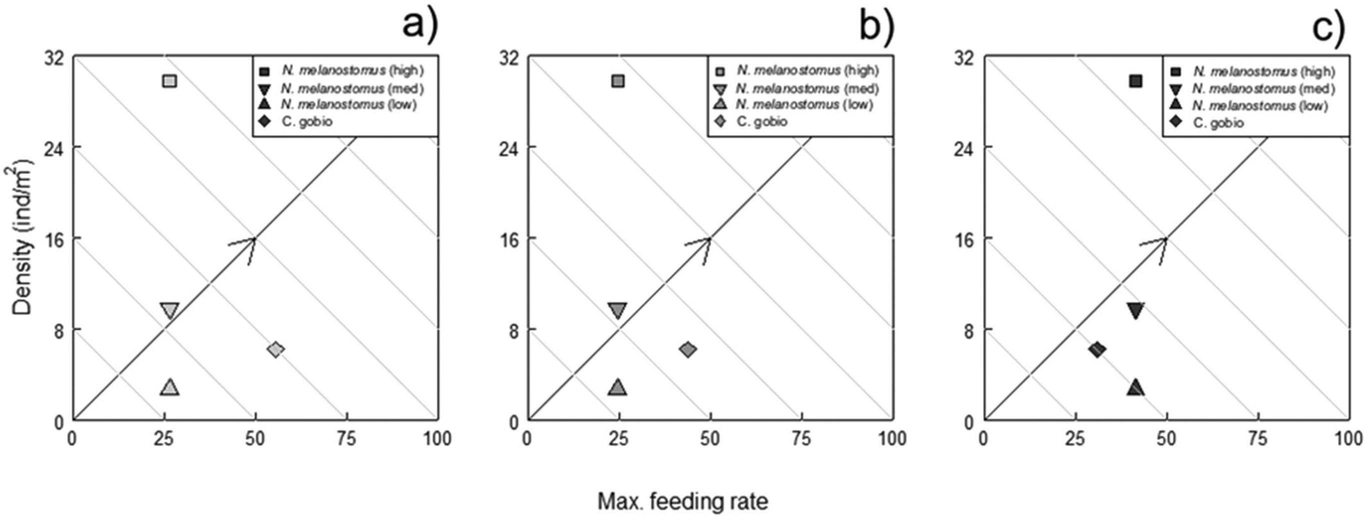

Fig. 2. Biplots showing Relative Impact Potentials of invasive round goby (*Neogobius melanostomus*) and the native bullhead (*Cottus gobio*) towards gammarid prey in the presence of different shell densities of dead *Corbicula fluminea*: 0 shells (a), 10 shells (b) and 20 shells (c). Each plot shows high, medium and low estimates of *N. melanostomus* density obtained from the Moselle river, France, as per Masson et al. (2018), with *C. gobio* data from the uninvaded Ru du Dragon, France, from the Fédération de Seine-Et-Marne Pour La Pêche et la Protection du Milieu Aquatique. See Table 2 for Relative Impact Potential (RIP) calculations, i.e. the product of fish maximum feeding rate and fish density. In this Figure, these two measures are presented on the x and y axes respectively, with impact increasing along the diagonal arrows from the bottom left of the plot to the top right corner.

when assessing ecological effects of these species. Although *N. melanostomus* feeding rates were suppressed to a lesser degree than *C. gobio*, both species were significantly impeded by benthic habitat structure overall, which may lessen their destabilising effects on prey populations. Moreover, we note that fish selected for the experiment were matched as closely as possible in terms of their total length and mouth gape height to enable quantification of species-specific differences unrelated to fish size and mouth gape. Yet, this may underestimate the ecological impacts of the invader that tends to grow larger than the native (Froese and Pauly, 2021). As such the feeding rate of larger adult *N. melanostomus* should also be considered in relation to invader-driven habitat complexity. Nevertheless, our experimental data provide an indication of the mechanism by which *N. melanostomus* can exploit parallel bivalve invasions, and further underpin the phenomenon of facilitative interactions among IAS.

Both of the assessed fishes inhabit similar habitat types (e.g. Janáč et al., 2018), with the presence of *N. melanostomus* having been linked to population declines of several species, such as mottled sculpin *Cottus bairdii* (Janssen and Jude, 2001), and river bullhead *Cottus perifretum* (Van Kessel et al., 2016). Although the impact of these negative effects appears to be region-specific, as *C. gobio* can maintain a stable population despite co-occurrence with *N. melanostomus* (Janáč et al., 2018). Nevertheless, *C. gobio* has a co-evolutionary relationship with freshwater communities in western Europe, and thus serves as an appropriate baseline for comparison of invader-driven ecological impacts (see Dick et al., 2017b; Dickey et al., 2021). Furthermore, as *N. melanostomus* can reach higher densities than *C. gobio*, the potential population-level ecological impact of the invader is predicted to be considerably greater than the native (Laverty et al., 2017; Dickey et al., 2020, 2021). Accordingly, while *C. gobio* might benefit from a mild facilitative effect at low *C. fluminea* densities, this benefit will diminish at population-level relative to *N. melanostomus*. Nevertheless, the same effect experienced by *N. melanostomus* at the highest shell abundance could magnify their ecological impact at greater invader population densities. Therefore, we propose that riverine habitat complexity may aid co-existence between *N. melanostomus* and *C. gobio*, and explain the persistence of *C. gobio* in some environments invaded by *N. melanostomus* (e.g. Janáč et al., 2018), despite the invader-driven exclusion of other fishes (e.g. Van Kessel et al., 2016). Yet the balance of this co-existence can be impacted by invader-driven habitat complexity, with negative consequences for native *C. gobio*. Already, several studies have shown that the presence of invasive bivalves can benefit other invaders and negatively impact native species in large freshwater ecosystems, such as the facilitation of dominance shifts for an invasive crayfish over a congeneric native in the Laurentian Great Lakes (Glon et al., 2017), as well as for invasive freshwater macrophytes spp. in Lough Erne (Crane et al., 2020). Nevertheless, further research is needed to elucidate the long-term effects of invader-driven habitat complexity across predator fish densities.

Overall, this study has shown that invader-driven habitat complexity can influence the feeding rates of both native and invasive predatory fishes, driving invader impacts on the broader community. Although the feeding rate of native *C. gobio* was greater than that of invasive *N. melanostomus* in the presence of sand and low shell abundances, it appears that *N. melanostomus* can better utilise higher shell abundances in terms of its maximum feeding rate and FRR value. This suggests the occurrence of a significant facilitative interaction that may contribute towards greater invader impact when scaled to the level of the population. We suggest future work to examine the emergent interactions between multiple IAS in terms of ecological impact and invasion success. In addition, this work emphasises the need to consider habitat complexity when calculating FRs as per capita consumption measured under simplified conditions is an idealistic rather than realistic approach.

CRediT authorship contribution statement

Neil E. Coughlan: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Visualization; Roles/Writing - original draft; Writing - review & editing.

James W.E. Dickey: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Visualization; Writing - review & editing.

Jaimie T.A. Dick: Conceptualization; Funding acquisition; Project administration; Supervision; Validation; Writing - review & editing.

Vincent Médoc: Conceptualization; Funding acquisition; Resources; Validation; Writing - review & editing.

Monica McCard: Conceptualization; Funding acquisition; Investigation; Validation; Writing - review & editing.

Gérard Lacroix: Funding acquisition; Project administration; Resources: Validation; Writing - review & editing.

Sarah Fiorini: Project administration; Resources; Validation; Writing - review & editing.

Alexis Millot: Project administration; Resources; Validation; Writing - review & editing.

Ross N. Cuthbert: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Visualization; Writing - review & editing.

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Ethics approval

Fish capture and transport were approved by the Direction Départementale des Territoires de la Moselle for the round goby (DDT 42) and the Direction Départementale des Territoires de la Seine et Marne (DDT 77) for the bullhead. All the procedures were conducted in accordance with appropriate European (Directive 2010/63/EU) and French national guidelines, permits and regulations regarding animal care and experimental use (B77-431-1). At the end of the experiments, bullheads were returned to their sampling site, whereas gobies were euthanised using MS-222 to meet European legislation on invasive alien species. All relevant protocol approvals were obtained prior to this research (see Supplementary Material for further detail).

Consent to participate

Not applicable.

Consent for publication

All authors have given approval for publication.

Availability of data and material

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Code availability

Not applicable.

Authors' contributions

NEC, JWED and RNC conceived the study, with NEC, JWED and RNC performing the experiments, conducting statistical analyses and preparing the initial manuscript, which was led by NEC. JTAD, VM, MMcC, GL, SF, and AM contributed vital input to the development of concepts within the final manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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